

The Metabolic Costs of Sound Production in Odontocete Cetaceans

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Award Number: N0001410IP20067

http://www.nwfsc.noaa.gov/research/divisions/cbd/marine_mammal/marinemammal.cfm

LONG-TERM GOALS

Animals often increase the amplitude (the Lombard effect), duration, and/or repetition rate of their acoustic signals as a strategy to help reduce the probability of masking from environmental sounds (NRC 2003). Although accumulating evidence from recent research (Scheifele et al. 2005, Holt et al. 2009, Parks et al. 2010) illustrates that several marine mammal species readily modify the parameters of their acoustic signals to compensate for masking noise, potential energetic costs of such compensation behavior are unknown. To our knowledge, there is no empirical data on the metabolic cost of sound production for any marine mammal species. Given that changes in vocal behavior in response to masking noise has been documented in several species, assessing the biological significance of these effects is paramount but also very difficult given the life histories of marine mammals. The Population Consequences of Acoustic Disturbance (PCAD) model has been proposed as a framework to address this challenging task (NRC 2005). Data on the energetic cost of dolphin vocalization from this study can be used to assess the biological significance of vocal compensation in response to sound exposure and populate transfer function 2 (transfer function between behavior change to life functions immediately affected) in the PCAD model.

OBJECTIVES

For the first year of this study (Phase 1), we aim to measure oxygen consumption in two captive bottlenose dolphins during sound production at relatively low to moderate levels and compare the metabolic costs of sound production to resting metabolic rates (RMRs) and metabolic costs of other activities, such as performing surface active behaviors (SABs) and/or swimming. This phase of our work is ongoing and will continue until the end of the 2010 calendar year. For the second year of this study (Phase 2, 2011), we propose to measure oxygen consumption in these individuals while they produce the same type of sounds but at different levels, durations, or repetition rates. These measurements will quantify the potential metabolic cost of vocal compensation as an anti-masking strategy in response to anthropogenic sound exposure.

Report Documentation Page				Form Approved OMB No. 0704-0188	
Public reporting burden for the collection of information is estimated to average 1 hour per response, including the time for reviewing instructions, searching existing data sources, gathering and maintaining the data needed, and completing and reviewing the collection of information. Send comments regarding this burden estimate or any other aspect of this collection of information, including suggestions for reducing this burden, to Washington Headquarters Services, Directorate for Information Operations and Reports, 1215 Jefferson Davis Highway, Suite 1204, Arlington VA 22202-4302. Respondents should be aware that notwithstanding any other provision of law, no person shall be subject to a penalty for failing to comply with a collection of information if it does not display a currently valid OMB control number.					
1. REPORT DATE 2010		2. REPORT TYPE		3. DATES COVERED 00-00-2010 to 00-00-2010	
4. TITLE AND SUBTITLE The Metabolic Costs of Sound Production in Odontocete Cetaceans				5a. CONTRACT NUMBER	
				5b. GRANT NUMBER	
				5c. PROGRAM ELEMENT NUMBER	
6. AUTHOR(S)				5d. PROJECT NUMBER	
				5e. TASK NUMBER	
				5f. WORK UNIT NUMBER	
7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES) NOAA NMFS Northwest Fisheries Science Center, 2725 Montlake Blvd. East, Seattle, WA, 98112				8. PERFORMING ORGANIZATION REPORT NUMBER	
9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)				10. SPONSOR/MONITOR'S ACRONYM(S)	
				11. SPONSOR/MONITOR'S REPORT NUMBER(S)	
12. DISTRIBUTION/AVAILABILITY STATEMENT Approved for public release; distribution unlimited					
13. SUPPLEMENTARY NOTES					
14. ABSTRACT					
15. SUBJECT TERMS					
16. SECURITY CLASSIFICATION OF:			17. LIMITATION OF ABSTRACT Same as Report (SAR)	18. NUMBER OF PAGES 9	19a. NAME OF RESPONSIBLE PERSON
a. REPORT unclassified	b. ABSTRACT unclassified	c. THIS PAGE unclassified			

APPROACH

The metabolic cost of sound production is being measured in two captive male Atlantic bottlenose dolphins (*Tursiops truncatus*) maintained at Dr. Terrie Williams' Mammalian Physiology Laboratory at the University of California, Santa Cruz, Long Marine Laboratory. These individuals were trained by Traci Kendall (Program Manager/Research Training Supervisor) and Beau Richter (Head Trainer) to produce sounds on command while stationed under a metabolic hood to measure oxygen consumption. The sounds of free-ranging Atlantic bottlenose dolphins have been described as clicks, whistles, buzzes, quacks, and pops (Jacobs et al. 1993). The trained sounds of the captive dolphins of the current study are representative of those found in wild, free-ranging populations.

Experimental sessions are conducted in the morning. The dolphins are fasted overnight before experimental sessions to eliminate the potential for the metabolic cost of digestion to confound oxygen consumption measurements. Thus, food rewards are given after the experimental session is complete and only one experimental session is conducted per dolphin per day. Briefly, each experimental session consists of one dolphin remaining at the water surface under the metabolic hood (details described in next paragraph) for one 10-minute period of rest (to determine baseline metabolic rate), followed by two consecutive one-min bouts of sound production (the two bouts are separated by 15-20 sec of silence), and concluding with a recovery period (at least 10 minutes, or until oxygen consumption values return to resting values). During all trials, the dolphins are acoustically monitored in real-time and their sounds are recorded for further analysis as described below. The total duration of the rest period, sound production period, and recovery period are recorded for each experimental session. Respirations are also recorded during each of the three periods so that respiration rates can be calculated for the dolphins during rest, sound production, and recovery. See figure 1 for a photograph taken during one experimental session.



Figure 1. Photograph taken during one experimental session showing the equipment set-up which includes the metabolic hood, the dolphin stationed under the metabolic hood, the acoustic recording equipment and operator, the dolphin trainer, and the assistant taking notes and recording respirations. During the trial the dolphin is acoustically monitored and all respirations are recorded during each of the three periods.

The method used for determining metabolic rates from oxygen consumption values are similar to those used previously on bottlenose dolphins (Williams *et al.* 1993) and northern elephant seals (Noren 2002). For this study, the rate of oxygen consumption ($\dot{V}O_2$) is being determined for quiescent dolphins stationed at the water surface and for the same dolphins producing sounds at the water surface. Air is drawn into the hood at a flow rate of 300 L min^{-1} . The flow rate is maintained such that the content of oxygen in the hood will remain above 20%. Water and CO_2 from subsamples of excurrent air from the hood are absorbed using Drierite and Baralyme, respectively, prior to entering the oxygen analyzer. The percentage of oxygen in the sample line is monitored continuously (FC-1B O_2 Analyzer, Sable Systems International) and recorded by a laptop computer every second during the experimental sessions. $\dot{V}O_2$ for resting and vocalizing dolphins will be calculated from the percentage oxygen data by respirometry software (Expedata data acquisition and analysis software, Sable Systems International). Dr. Dawn Noren is responsible for collecting and analyzing the respiration rate and oxygen consumption data.

Sound production during all trials is acoustically monitored in real-time and also recorded using calibrated equipment to quantify the sound pressure level (in dB rms re: 1 microPa), duration (in sec) and repetition rate (phonations/min) of the phonations of the dolphins. The recording equipment includes two calibrated Reson hydrophones (TC 4033 and TC 4013). Calibration is checked on a

regular basis with a pistonphone connected to a custom adaptor (42AA with RA78, GRAS Sound & Vibration). Both hydrophones are connected through a series of filters and amplified (Reson VP 2000) and digitized using the MOTU traveler at a sampling rate of 96 kHz and then recorded (2 channels) and monitored in real-time in the time and frequency domain using SpectraPlus 5.0 Software (Pioneer Hill). Hydrophone placement is the same during all periods (rest, sound production, and recovery) of each experimental session. Dr. Marla Holt is responsible for collecting and analyzing the acoustic data.

WORK COMPLETED

Due to a delay in FY2010 funding, only one trip (July 11-17, 2010) to Dr. Terrie Williams' Mammalian Physiology Laboratory at the University of California, Santa Cruz, Long Marine Laboratory for data collection has been accomplished so far. During this trip, a total of 12 trials were run (6 trials per each dolphin), technical issues were resolved, and the final protocol for the experimental sessions were determined. Two trials of the final experimental session protocol were conducted on each of the two dolphins. During all trials acoustic, metabolic, and respiration data were collected. Acoustic and metabolic data have been visually inspected and respiration rate data have been analyzed. Two additional data collection trips are scheduled for October 2010, and a fourth trip, if needed, is scheduled for December 2010.

RESULTS

The goals of the first data collection trip were to assess the quality of the dolphins' vocalizations, observe the dolphins' behavior while vocalizing and resting under the metabolic hood, and to determine the final protocol to be used for the remainder of the trials. A total of 12 trials (6 trials per each dolphin) were conducted; and acoustic, metabolic, and respiration data were collected during all trials. The final experimental protocol described above was successfully run for 4 trials (2 trials per each dolphin). Each dolphin produced consistent sounds during his vocal bouts, but the sounds produced differed between the two dolphins. Specifically, Primo produced his signature whistle while Puka produced what we describe as a pulsed squawk or squeak-like sound as illustrated in the spectrograms of Fig. 2. Puka's pulsed sound is similar to the quack sounds described by Jacobs et al. (1993).

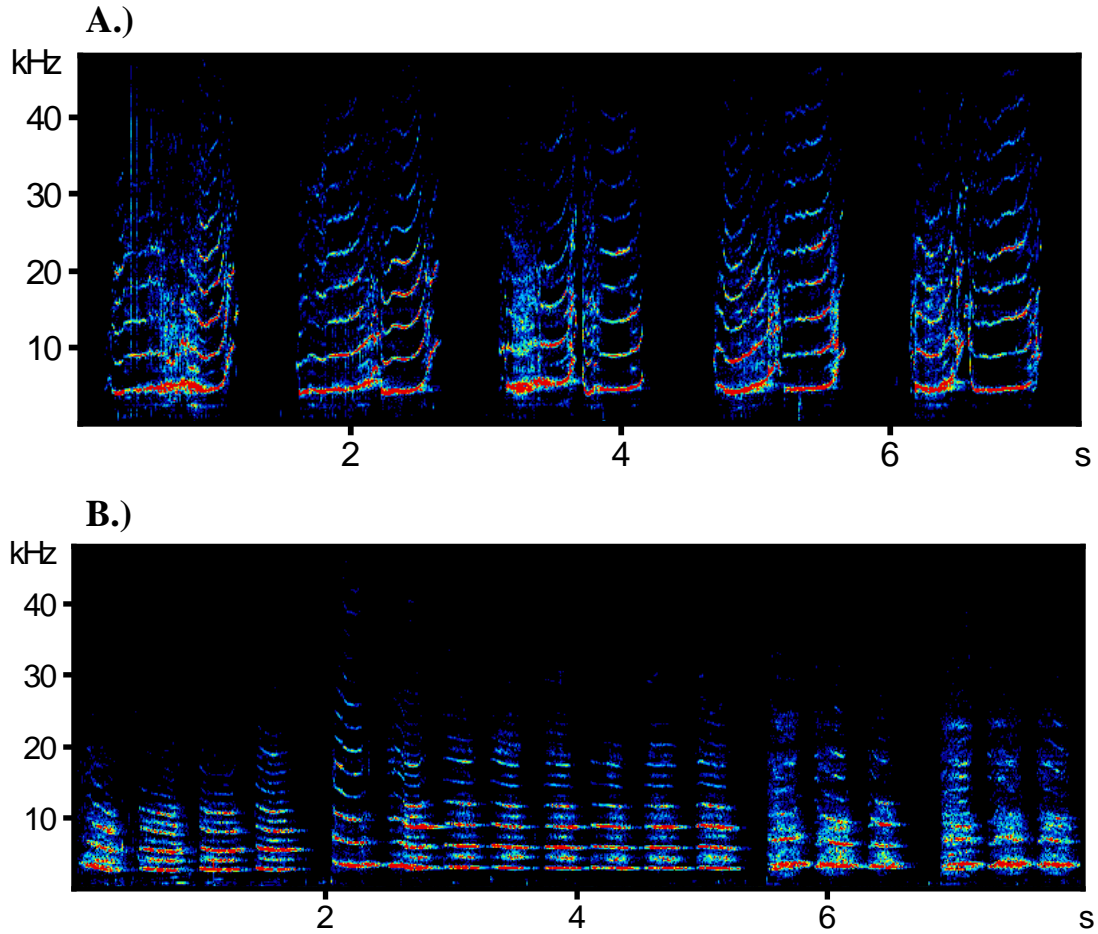


Figure 2. *Spectrograms showing 8 second examples of vocalizations performed by A.) Primo which are five of his signature whistles and B.) Puka which are 18 pulsed squeak-like sounds. Both spectrograms show visual representations of vocalizations performed during oxygen consumption data collection with time from 0-8 seconds on the x-axis and frequency from 0-48 kHz on the y-axis. The colors denote relative level or amplitude differences with red indicating higher levels and blue indicating lower levels.*

Preliminary visual inspection of the oxygen consumption data suggests that both types of vocalizations impact a measurable metabolic cost to dolphins (Fig. 3). Yet, we did not observe associated changes in respiration rates (Fig. 4). Note that the sample size is still very small so results are preliminary and should be taken with caution.

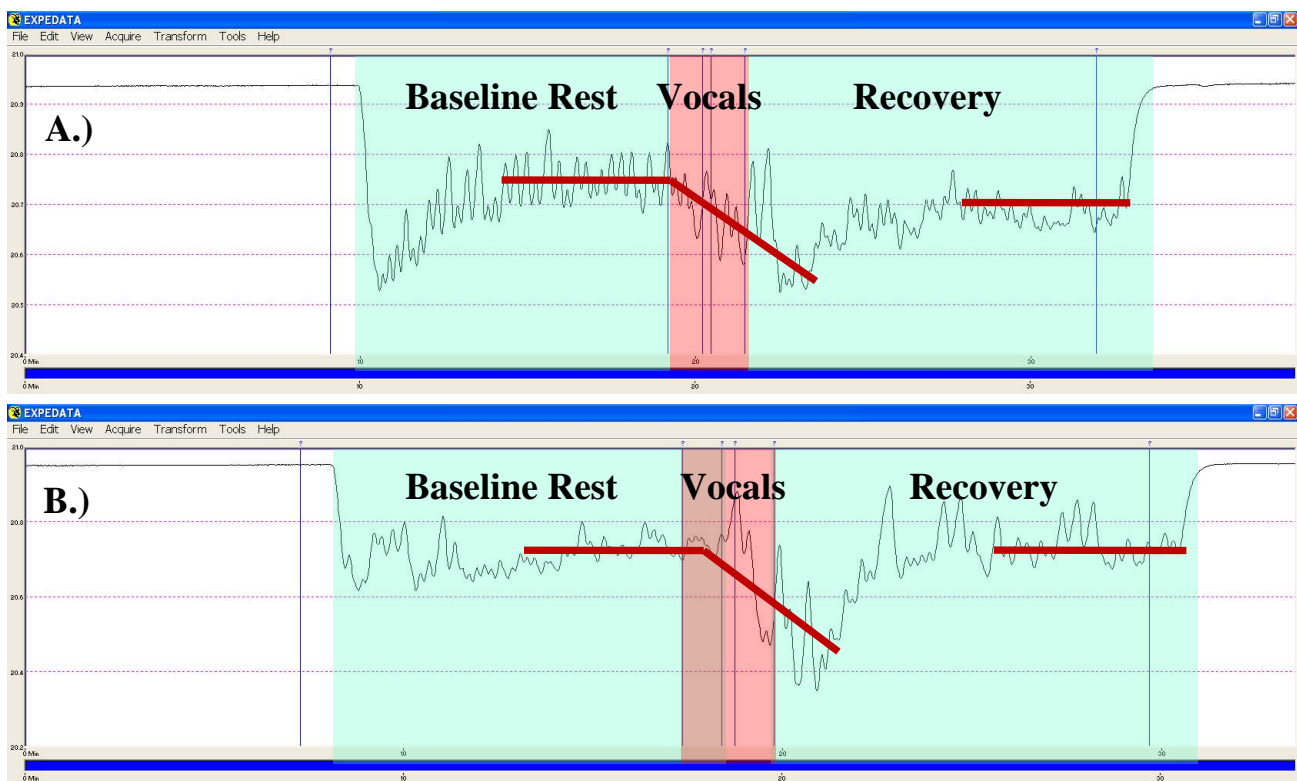


Figure 3. Screen shots from the Expedata analysis program (Sable Systems International) showing the concentration of oxygen (%) in the subsample of air from the metabolic hood in relation to time for one experimental session for A.) Primo producing his signature whistles (Fig. 2A) and B.) Puka producing pulsed squeak-like sounds (Fig. 2B). The three components of the experimental session (baseline rest, vocal bouts, and recovery) are labeled and shaded. Baseline rest and recovery periods are shaded in cyan while the vocalization period (two consecutive one-min vocal bouts) is shaded in red. For Primo (A), average percent oxygen at baseline (horizontal red line within the first cyan shaded region) was approximately 20.75%. Percent oxygen declined (indicating an increase in oxygen consumption) during the vocal bouts (diagonal red line within the red shaded region) to a low of approximately 20.55%. Average percent oxygen after recovery (horizontal red line within the second cyan shaded region) was approximately 20.7%. For Puka (B), average percent oxygen at baseline (horizontal red line within the first cyan shaded region) was approximately 20.75%. Percent oxygen declined (indicating an increase in oxygen consumption) during the vocal bouts (diagonal red line within the red shaded region) to a low of approximately 20.45%. Average percent oxygen after recovery (horizontal red line within the second cyan shaded region) was approximately 20.75%.

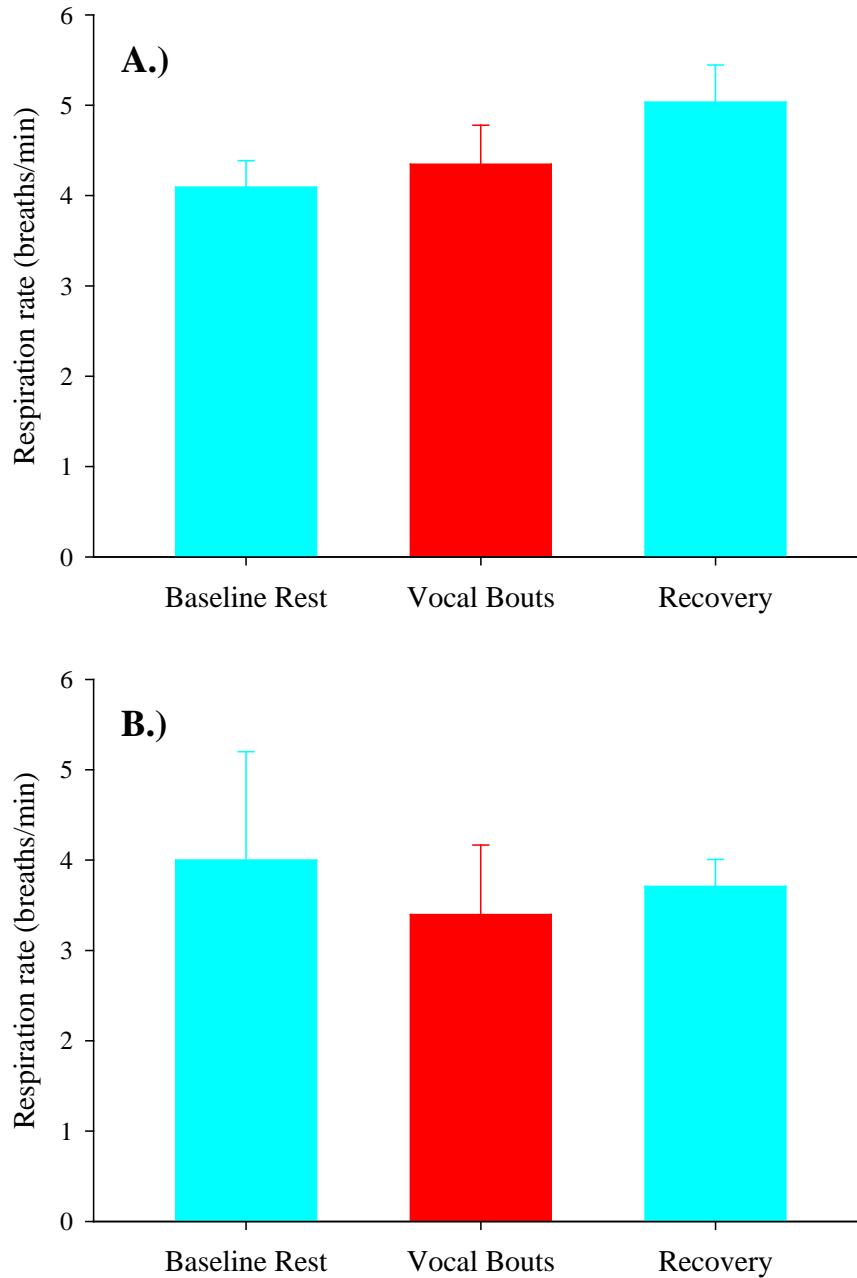


Figure 4. Average respiration rate (breaths/min, + 1 SEM error bar) during the baseline rest, vocal bouts, and recovery phases from two experimental sessions each for A.) Primo and B.) Puka. The three components of the experimental session (baseline rest, vocal bouts, and recovery) are labeled. Baseline rest and recovery periods are shaded in cyan while the vocalization period (two consecutive one-min vocal bouts) is shaded in red. For Primo (A), average respiration rate during baseline rest is 4.1 ± 0.3 , during vocal bouts is 4.3 ± 0.4 , and during recovery is 5.0 ± 0.4 breaths/min. For Puka (B), average respiration rate during baseline rest is 4.0 ± 1.2 , during vocal bouts is 3.4 ± 0.8 , and during recovery is 3.7 ± 0.3 breaths/min. For both dolphins, respiration rates recorded during each of the three phases of the experimental session do not differ ($p > 0.05$).

The preliminary data demonstrate that this method is successful in assessing the metabolic cost of sound production in odontocete cetaceans. The initial analysis suggests that there is a measurable energetic cost of sound production in bottlenose dolphins, and that it may take up to 5-10 min for dolphins to recover to baseline oxygen consumption values following two consecutive one-min vocal bouts. Furthermore, we found that respiration rates did not change during the three components of the experimental session. These results are preliminary but if this pattern holds with an increased sample size, it suggests that increased oxygen consumption during vocal bouts is probably not due to changes in breathing patterns; rather, it is likely due to an increase in metabolic demand related to the production of sound. With the additional data that will be collected during future trials, we will be able to quantify these costs (and the costs of vocal compensation such as increasing amplitude, duration or repetition rate as we propose to do in phase 2) and assess whether they are biologically significant.

IMPACT/APPLICATIONS

Currently, there is no empirical data on the metabolic cost of sound production in any marine mammal species. Theoretical assessments of such costs need to factor in variables such as efficiency factors and the relationships between physiological processes and metabolic costs associated with behaviors given that they often do not simply scale according to linear relationships. However, such data needed for theoretical modeling on this topic are also lacking. Empirical data collected from this study will provide valuable information about sound production costs in odontocetes including costs of modifying acoustic signals in response to anthropogenic sound exposure. For example, if there are significant costs of such behavior as an anti-masking strategy then these effects can impact the energy balance of individuals that in turn affect survival and reproduction. Specifically, this study will provide important input data to populate transfer function 2 in the PCAD model which can then be used to assess the biological significance of such responses to anthropogenic sound exposure.

RELATED PROJECTS

Dr. Terrie Williams' Marine Mammal Physiology Project involves other studies on the two dolphins used in this study. The goal of one related study is to assess the changing energetic demands in cetaceans, and in particular, determine the principle factors in regulating the variable metabolism of cetaceans over the seasons.

http://www.mmpp.ucsc.edu/The_Marine_Mammal_Physiology_Project/Home.html

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PUBLICATIONS

Noren, D.P., Dunkin, R.C., Williams, T.M., Holt, M.M. The energetic cost of behaviors performed in response to vessel disturbance: one link in the PCAD Model. In: Anthony Hawkins and Arthur N. Popper, Eds. *The Effects of Noise on Aquatic Life*. [in press]

HONORS/AWARDS/PRIZES

Dr. Dawn Noren, NOAA NMFS Northwest Fisheries Science Center, partial travel award (600 Euros) for oral presentation, “The energetic cost of behaviors performed in response to vessel disturbance: one link in the PCAD Model” at the 2nd International Conference on the Effects of Noise on Aquatic Life in Cork, Ireland, August 2010.